The biology of mycorrhiza in the Ericales

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The types of mycorrhizal structure seen in the Ericaceae and in the closely related families Pyrolaceae and Monotropaceae are reviewed briefly. Ericoid, arbutoid, and monotropoid mycorrhizas are characterized. The processes of infection and of establishment of the mature ericoid mycorrhizal association are discussed from the structural, ultrastructural, and functional viewpoints. Infection provides an enhancement of N and P supply to the host plant. The enhancement of N supply arises from an improved exploitation of "available" ammonium ions and from the capacity, provided exclusively by the mycorrhizal fungus, to utilize simple organic nitrogen compounds. The endophyte also provides increased phosphatase activity and access to what are otherwise only slightly available organic sources of phosphates. In addition to enhancement of host nutrition in circumstances of low nutrient availability, it is shown that ericoid mycorrhizal infection leads to restriction of uptake of metallic elements when these are present in high concentration. Infection thus provides resistance to heavy metal toxicity. The significance of these observations is discussed in relation to the capacity of plants with ericoid mycorrhizas to exploit marginal ecological situations in temperate, boreal, subarctic, and alpine regions throughout the world.

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L'auteur examine brièvement les types de structures mycorhiziennes qu'on observe chez les Ericacées et chez deux familles qui leur sont étroitement apparentées, les Pyrolacées et les Monotropacées. Les processus d'infection et d'établissement de l'association mycorhizienne érocoïde sont discutés des points de vue structural, ultrastructural et fonctionnel. L'infection augmente l'apport de N et de P à la plante-hôte. L'accroissement de l'apport d'azote provient d'une meilleure exploitation des ions ammonium "disponibles" et de la capacité, exclusive au champignon mycorhizien, d'utiliser des composés organiques azotés simples. L'endophyte provoque aussi une augmentation de l'activité phosphatasique et permet d'exploiter des sources de phosphates organiques qui seraient autrement très peu disponibles. En plus d'améliorer la nutrition de l'hôte lorsque la disponibilité des éléments nutritifs est faible, l'infection mycorhizienne éricoïde amène une diminution de l'absorption des éléments métalliques quand ceux-ci sont présents dans le sol en concentrations élevées. L'infection fournit donc une résistance à la toxicité due aux métaux lourds. La signification de ces observations est discutée en relation avec la capacité des plantes pourvues de mycorhizes éricoïdes d'exploiter des habitats écologiquement marginaux dans les régions tempérées, boréales, subarctiques et alpines du monde.

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Introduction

The order Ericales is recognized as a natural group of closely related families (Engler and Prantl 1897; Cronquist 1968). Members of the order (Table 1) have a worldwide distribution, some families, notably the Ericaceae, having representatives which occur as dominant plants over vast areas of heathland in the Northern Hemisphere. In addition to their ecological significance, other genera such as *Rhododendron* and *Erica* are widely cultivated as ornamental plants and some *Vaccinium* species produce economically important fruit crops. While the aboveground parts of members of the order show considerable morphological diversity, the root systems of those representatives that have so far been systematically examined can be divided into two groups with relatively uniform structural features, each group being characterized by the possession of a particular type of mycorrhiza development. Most genera in the family Ericaceae have an entirely endomycorrhizal association of a characteristic type known as an "ericoid" infection (Harley 1969). Remaining members of the Ericaceae and most of the Pyrolaceae have an ect–endo infection, in which, in addition to intracellular penetration, there is a fully formed Hartig net and occasionally a fungal sheath. This type of mycorrhiza, which has been termed "arbutoid," is in some ways structurally intermediate between the endotype and ectotype and some of the fungi involved in formation of arbutoid mycorrhizas can also form typical ectomycorrhizas in a range of tree species (Zak 1974, 1976*a*, 1976*b*). Recent studies (Duddridge and Read 1982*a*) have shown that the achlorophyllous plant *Monotropa* has a distinctive mycorrhizal structure, for which the term "monotropoid" is proposed.

The uniformity of root structure is paralleled by uniformity of ecological situations in which ericaceous plants become dominants. With few exceptions they are restricted to soils of low pH, high organic matter content, and low available nutrient status. This parallelism suggests that the characteristic mycorrhizal associations have evolved as a response to the specific stresses of this type of soil environment. Recent research has

TABLE 1. Some taxonomic, geographic, and mycorrhizal relationships within the Ericales

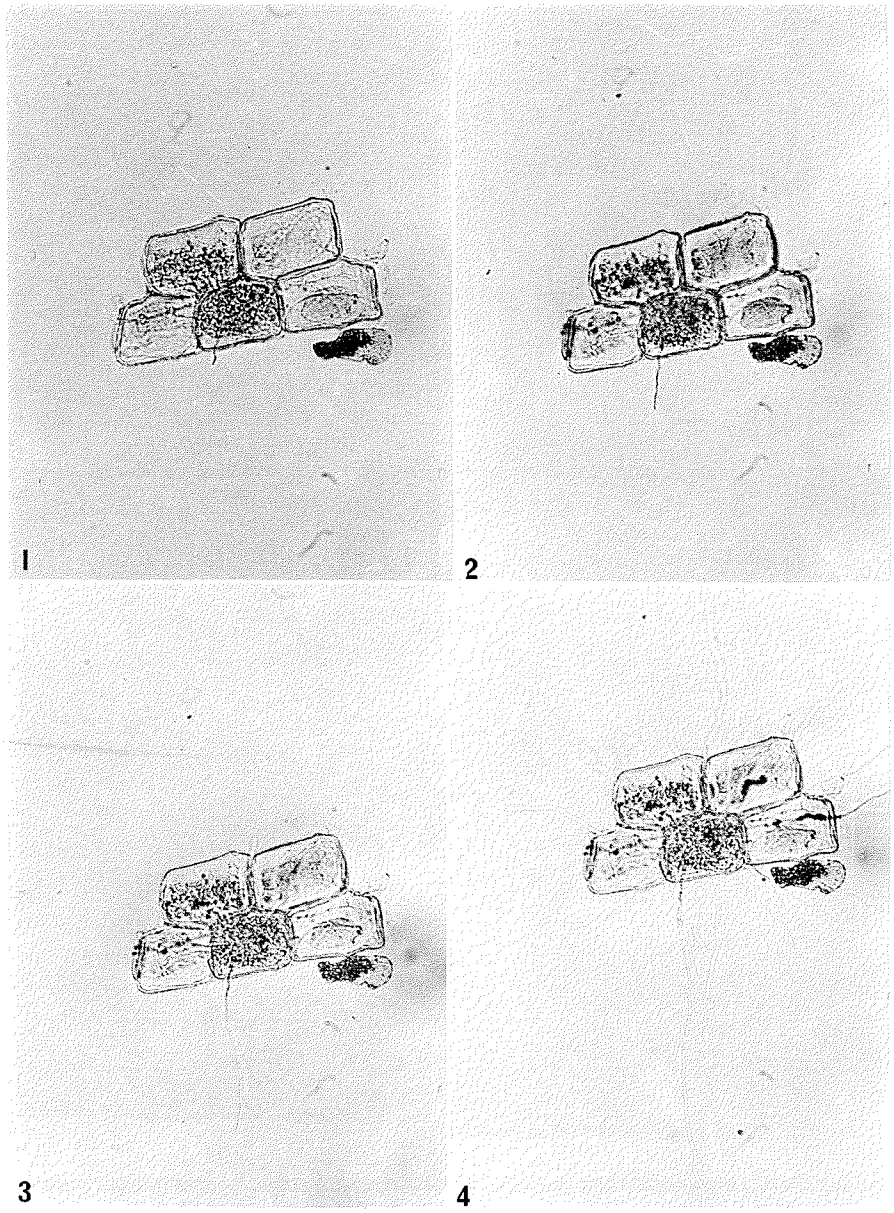
Order	Family	Important genera	Distribution	Mycorrhizal status
Ericales	Clethraceae	Clethra	Restricted to central America and SE Asia	Not known
	Grubbiaceae	Grubbia	Restricted to southern Africa	Not known
	Cyrillaceae	Cyrilla, Cliftonia, Purdiaea	Restricted to central America	Not known
	Ericaceae	Arbutus, Arctostaphylos, Cassiope, Calluna, Erica, Gaultheria, Kalmia, Ledum, Rhododendron, Vaccinium	Worldwide	Mycorrhizal. Some "arbutoid" but mostly with "ericoid" infection
	Epacridaceae	Dracophyllum, Epacris, Richea, Styphelia	Restricted to southern South America, Indonesia, Australasia	Mostly not known. Some "ericoid" infection
	Empetraceae	Ceratiola, Corema, Empetrum	Throughout northern hemisphere and in southern South America	Mycorrhizal, Ericoid
	Pyrolaceae	Chimaphila, Moneses, Pyrola, Orthilia	Boreal and subarctic distribution in northern hemisphere	Mycorrhizal. Mostly arbutoid
	Monotropaceae	Monotropa, Pterospora		Monotropoid

begun to elucidate some of the functional relationships between the ericaceous host plant, the associated fungus, and the soil environment.

Ericoid mycorrhizas, historical and structural aspects

Much controversy surrounded the early studies of the occurrence of ericoid mycorrhizas and protracted arguments over the nature and development of infection served to distract attention from the more important question of the role of mycorrhiza in the growth and nutrition of the host. These controversies have been fully reviewed by Harley (1969) and only a brief account of their development is presented here. Ternetz (1907) reported that the mycorrhizal fungus of *Calluna* fixed atmospheric nitrogen and that seedlings of the host could not be grown without fungal infection. In a series of reports Rayner (1915, 1925, 1929) added support to this view. She stated that while surface-sterilized seed of *Calluna* and *Vaccinium* could germinate normally, later development of the shoot and root was inhibited in the absence of the fungus. She also believed that infection of the root extended into the shoot system and that it eventually reached the seed coat so that at germination the emerging radicle was immediately penetrated by the appropriate fungus to produce a "systemic" infection. Such a process was also described by Addoms and Mounce (1931, 1932). Workers at the time, notably Knudson (1929, 1933) in America and Christoph (1921) in Europe, produced results which strongly contradicted the thesis that systemic infection was either normal or necessary for seedling development and it has been repeatedly shown since that normal development of ericaceous seedlings can be achieved in completely sterile conditions (Friesleben 1933, 1934, 1936; Bain 1937; Molliard 1937; Singh 1974; Pearson and Read 1973). In addition, there appears to be not a single authenticated report of the isolation of the mycorrhizal fungus from any part of the ericaceous plant other than the root itself. Despite Rayner's assertion that systemic infection was a normal feature of ericaceous plants, she provided no confirmatory evidence in the form of backinoculation to synthesize mycorrhizas. Doak (1928) was the first to report isolation of an endophyte from the roots and backinoculation to produce mycorrhizas. Later Friesleben (1936) showed that fungi isolated from *Vaccinium* would form mycorrhizas not only with their original hosts but with a wide range of other ericaceous plants including *Calluna* and *Erica*. The endophytes thus appeared to show little host specificity. This feature has since been confirmed by Pearson and Read (1973), who showed that the mycorrhizal fungus isolated from any species with ericoid mycorrhizas will readily form mycorrhizas with other ericoid hosts.

Both Ternetz and Rayner believed that the mycorrhizal fungus of ericoid plants was a member of the genus *Phoma*. Ternetz (1907) isolated this fungus from the roots of several ericaceous plants and called it *Phoma radicis*. Rayner (1915) found only common soil fungi in the roots of *Calluna* and proceeded to obtain most of her isolates from the shoots and seeds, which she believed also to contain the mycorrhizal fungus. From these she obtained a pycnidium-bearing fungus, which was again referred to the genus *Phoma* and called *P. radicis*. None of the *Phoma* isolates was ever shown to produce typical



FIGS. 1–4. Stages in the emergence of the mycorrhizal fungus from an infected cortical cell after serial washings and maceration of a *Calluna* root. ×750.

ericoid mycorrhizas. This fact, coupled with the knowledge that *Phoma* is a common colonist of moribund tissue in a wide range of plant species, strongly indicates that it is not the mycorrhizal fungus of ericoid mycorrhizas.

The only procedure which will demonstrate unequivocally that a fungus is truly mycorrhizal is to isolate it as it emerges from the infected cell and then to inoculate the isolate into aseptically grown seedlings to ensure that it produces a normal mycorrhizal association. Stages in the use of these isolation (Figs. 1–4) and reinoculation (Fig. 7) procedures are shown. Most workers who have systematically isolated endophytes from roots and then reinfected seedlings have reported that the fungus is sterile and described their isolates in terms of different culture characteristics. For example, Friesleben (1934) identified strain differences, while Bain (1937) and Burgeff (1961) described colour and growth form differences which distinguished their isolates. Despite these differences a number of features of all these isolates are held in common, and it may be more advantageous to stress the similarities rather than the

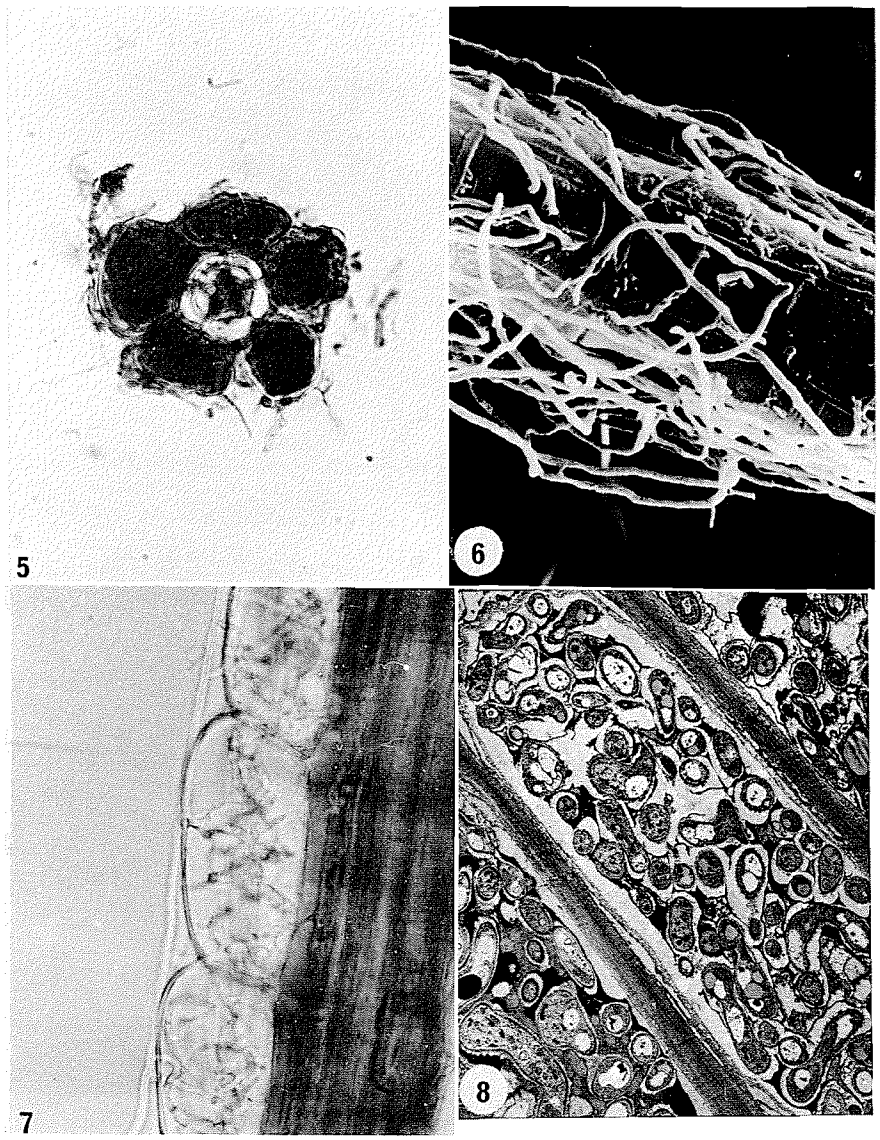


FIG. 5. Transverse section of a mycorrhizal hair root of *Calluna vulgaris*. A single layer of inflated cortical cells each filled by endophyte hyphae surrounds the narrow central stele. ×600. FIG. 6. The surface of the hair root of *Calluna* as revealed by scanning electron microscopy. Endophyte hyphae can be seen passing over the surface and penetrating the outer cortical cell walls. ×960. FIG. 7. Lateral view of hair root of *Calluna* showing early stages of mycorrhizal infection of outer cortical cells after inoculation of irradiated soil by the endophyte. ×1200. FIG. 8. Low magnification TEM of three outer cortical cells of a hair root of *Rhododendron ponticum*. Each cell is an individual infection unit and the associations are at a different stage of development. The bottom left-hand cell shows the youngest infection with active host cytoplasm. Some deterioration of host cytoplasm is seen in the central cell and this has advanced so that little structural integrity remains in the infection unit of the cell in the upper right side of the figure. Fungal integrity is maintained in all three cells. ×2800.

small differences between isolates. The most important common feature of course is the capacity to form mycorrhizas. Further than this, however, even in cultures common features are found. Thus the isolates are normally slow growing on nutrient agar and have a colour in the range grey, grey–brown, to vinaceous fawn. The growing edge of the culture is characteristically white when viewed from the under side of the petri dish. An important negative feature is that pycnidia are not formed by any such isolates. It has now been shown (Read 1974) that typical ericoid endophytes of the type described above can be stimulated to fruit under

some circumstances. The fungus produces orange apothecia up to 1 mm in diameter, which are initially cup shaped but become flattened discs at maturity. The fungus is an ascomycete and has been named *Pezizella ericae* Read. Ultrastructural studies of mycorrhizal roots of *Calluna* and *Vaccinium* have confirmed that the normal endophyte is an ascomycete (Bonfante-Fasola and Gianinazzi-Pearson 1979; Duddridge and Read 1982*b*).

Other fungi have been observed to be closely associated with ericaceous plants. Among these the most frequently reported is the basidiomycete *Clavaria argillacea* (Gimingham 1960; Seviour et al. 1973; Englander and Hull 1980). Experiments of Englander and Hull have confirmed that the association is indeed a close one, in which exchange of nutrients between the partners can occur. It is difficult, however, to ascertain the true nature of this relationship because attempts to culture the fungus have so far failed. Without mycorrhizal synthesis it is not possible to determine whether the relationship occurs at the level of the rhizosphere or the healthy living host cell or is a mildly parasitic infection of moribund tissue. All such associations could lead to transfer of nutrients between the partners. There is clearly a need for further investigation of the nature of the occasional association between basidiomycete hyphae and the cells of ericoid roots, especially since Bonfante-Fasola (1980) reports that the general organization of basidiomycete-infected cells of *Calluna vulgaris* closely resembles that of the more usual ascomycete endophyte.

The structure of ericoid mycorrhizas as revealed by the light microscope

The ericoid type of mycorrhiza is found in those members of the Ericales which have a diffuse root system in which the laterals lack root hairs but are themselves sufficiently fine to be termed "hair roots" (Beijerinck 1940). The important genera *Calluna*, *Erica*, *Rhododendron*, and *Vaccinium* have roots of this kind. Transverse sections of such roots taken just behind the apex reveal only one to three layers of cortical cells, the number varying according to species, surrounding a narrow central stele. (Fig. 5). The anatomy of these roots has been described in detail by Burgeff (1961). In an established seedling root system in nature most of the mature outer cortical cells of the root become infected by the mycorrhizal fungus (Read and Stribley 1975). When the root system is actively extending, the apical meristem is normally free of infection, as are those older regions of more mature root systems in which suberisation has commenced. Most workers apart from Rayner have agreed that infection arises from penetration through the outer cell wall rather than by lateral spread of the fungus from cell to cell (Fig. 7). Each cell can thus be considered as an individual infection unit. Once within the cell the fungus proliferates to form what have been described as hyphal coils, hyphal complexes, or arbuscules (Rayner 1915; Gordon 1937; Bain 1937; Burgeff 1961; McNabb 1961; Singh 1974). Detailed study of intracellular hyphal development is almost beyond the power of resolution of the light microscope and for this reason analysis of intracellular events has usually been a mixture of observation and speculation. Most workers have described some form of "digestion," "phagocytosis," "lysis," or "autolysis" of the hyphal complexes. Both Rayner (1925) and Burgeff (1961) described such processes in detail.

Inherent in this type of description is the assumption that in the course of digestion nutrients are released from the fungus and passed to the healthy host cell. In such circumstances digestion would be the critical functional event in the relationship between fungus and host. Recent studies of ericoid mycorrhizas by transmission electron microscopy (TEM) have revealed that the sequence of events involved in degeneration of the infection unit is not the same as that described above and have necessitated a reappraisal of these critical stages of the relationship.

The structure of ericoid mycorrhizas as revealed by electron microscopy

Transmission electron microscopy studies of mature infection units (Nieuwdorp 1969; Bonfante-Fasola and Gianinazzi-Pearson 1979; Peterson *et al.* 1980) have shown that intracellular hyphae retain a discrete structural integrity within the host cell. In addition, Bonfante-Fasola and Gianinazzi-Pearson observed some deterioration in the appearance of host cytoplasm when there was no loss of integrity in the fungus. In a detailed chronological analysis of the sequence of events from infection of the host cell through to collapse of the association it has now been confirmed (Duddridge and Read 1982) that breakdown begins with deterioration of the host rather than the fungal tissue. Seedlings of *Rhododendron ponticum* were grown either in soil partially sterilized by γ-irradiation and then inoculated with the endophyte or in soil freshly collected from underneath *Rhododendron* bushes. Scanning electron microscopy (SEM) showed surface colonization of roots in irradiated soil after 3 weeks and in natural soil after 4 weeks. Penetration of the cortical cells followed immediately (Fig. 6). Once within the cell the fungal hyphae proliferate extensively. The host plasmalemma invaginates to envelope each branch of the invading fungus but is separated from the fungal cell wall by a thin electron-lucent layer, the so-called interfacial matrix (Fig. 9). This contains electron-dense flocculent material, which appears to be made up of pectic material (Duddridge 1980). The SEM and TEM studies have confirmed that infection is through the outer wall of the cortical cell so that each cell is an individual infection

FIG. 9. High magnification TEM view of intracellular hyphae (IH) within the host cortical cell of *Rhododendron*. The interfacial matrix (IM) between host plasmalemma (HP) and fungal wall (FW) is clearly visible, as is the electron-dense, probably pectic material within it. Both host (HC) and fungal (FC) cytoplasm are packed with ribosomes and have numerous mitochondria (M). There is little evidence of vacuolation. × 23 940. FIG. 10. Transmission electron microscope view of early stage of breakdown of the association. Host cytoplasm is degenerating (DHC) and contains few organelles. The interfacial matrix is indistinct, probably because the host plasmalemma is losing its integrity. The fungal hyphae still have abundant mitochondria. There is some increase on vacuolation of the intracellular hyphae (IH) and polyphosphate granules (PPG) are seen in some of the vacuoles. ×9675.

unit. For this reason even adjacent cells may have infections which are of different ages (Fig. 8). When infection of the host cell is mature, its volume is almost completely occupied by fungal hyphae and little or no vacuolar area is visible. Outside of the electron-lucent zone the hyphae are sheathed by host cytoplasm, which is packed with ribosomes and mitochondria, suggesting that at this stage the unit is the site of considerable physiological activity (Fig. 9).

The first sign of breakdown observed by Duddridge and Read (1982*b*) was a loss of structural integrity of the host organelles, particularly the mitochondria. Host cytoplasm itself then degenerates and as it does so, the electron-lucent area between the host plasmalemma and fungal cell wall becomes progressively wider. The integrity of the host plasmalemma is finally lost and most of the host organelles have degenerated before fungal deterioration is seen (Fig. 10). Evidence of deterioration in the fungal hyphae is seen in the form of an increase in the size of their vacuoles, but this occurs only in the later stages of host degeneration. Final breakdown of the fungus is not complete until after the collapse of host cell integrity. At the end of the breakdown process therefore the cell is empty apart from the debris of its earlier occupation. The first indication of breakdown was observed 8 weeks after inoculation and hence about 4 weeks after penetration in inoculated soil and about 11 weeks after planting into natural soil. The differences of timing are probably attributable to differences in the vigour of the partners in the two systems. Both fungus and host were much more active in the irradiated soil environment.

The events revealed by sequential TEM analysis are thus distinct from those previously described from light microscope studies. Since breakdown occurs first in host cytoplasm, nutrient transfer either from fungus to host or in the reverse direction must take place during the period of a few weeks after infection when both partners have full structural and hence presumably physiological integrity. This means that the active lifespan of the individual infection unit is not more than 5 or 6 weeks. In addition, the notion of digestion or lysis of the fungus by the host is not tenable.

Ultrastructural analysis also provides information concerning the taxonomic position of the fungal endophyte. Bonfante-Fasola and Gianinazzi-Pearson (1979) showed that the intracellular hyphae of *Calluna* contained simple septal pores indicting ascomycete affinities. In the course of examination of material from a wide range of ericaceous species including some from southern Africa Duddridge (1980) also found only hyphae with simple septal pores in an intracellular position, though dolipore septa were occasionally seen in rhizosphere hyphae. Both Bonfante-Fasola (1980) and Peterson *et al.* (1980) have observed hyphae with dolipore septa within ericoid cortical cells. Further analysis of the status of such infection should be made at the ultrastructural and synthesis levels. Careful discrimination between cytologically normal and abnormal associations is necessary because different types of biotrophic or even necrotrophic relationships may be involved in different host–endophyte systems.

Arbutoid mycorrhizas, historical and structural aspects

Detailed description of arbutoid mycorrhizas was first provided by Rivett (1924), who examined the roots of *Arbutus unedo*. It is now known that structures similar to those described by Rivett occur in *Arctostaphylos* (Friesleben 1936; Zak 1976*b*; Largent *et al.* 1980) and that they are also found in the Pyrolaceae (Luck 1940, 1941; Lihnell 1942; Largent *et al.* 1980). While most ericaceous species produce either ericoid or arbutoid mycorrhizas, some, for example *Leucothoe daviseae*, apparently have the capacity to yield both types (Largent *et al.* 1980), though it is not clear whether both infections occur on the same plant or even in the same locality. The essential feature of the arbutoid mycorrhiza is the possession of both a Hartig net and intracellular penetration by the fungus. The level of sheath development is a variable feature, which appears to depend at least to some extent upon local soil characteristics. Most of the early reports suggested that the fungi of arbutoid mycorrhizas were basidiomycetes and this has since been confirmed in pure culture syntheses (Zak 1974, 1976*a*, 1976*b*) and in a recent ultrastructural study (Duddridge 1980). No detailed EM analyses of this type of association have been reported, but in a preliminary examination of the roots of *Pyrola rotundifolia* ssp *maritima* using both SEM and TEM, Duddridge (1980) has shown that while the sheath was poorly developed in very young roots the outer hyphae of the Hartig net produced a reticulate patterns which marked the outer radial walls of the cortical cells (Fig. 12). These hyphae normally have a conspicuous clamp connection. Transverse sections examined by TEM reveal a fully formed underlying Hartig net and that the cortical cells adjacent to the Hartig net are occupied by hyphae, each of which is invested by host plasmalemma. The intracellular infection is thus structurally comparable with that seen in ericoid mycorrhizas. One distinguishing feature is that the internal hyphae frequently possess dolipore septa (Fig. 14), which confirms the observation of Zak that the fungi involved are probably similar to those forming ectomycorrhizas in forest trees. More recently J. Duddridge (unpublished data) has examined the mycorrhiza of *Arctostaphylos uva ursi*. Scanning electron microscope pictures show a well-developed sheath in this plant (Fig. 11), and Hartig net and intracellular hyphae again with dolipore septa (Fig. 13) are seen in sections examined by TEM.

Monotropoid infection, historical and structural aspects

The mycorrhizal relationships of the achlorophyllous

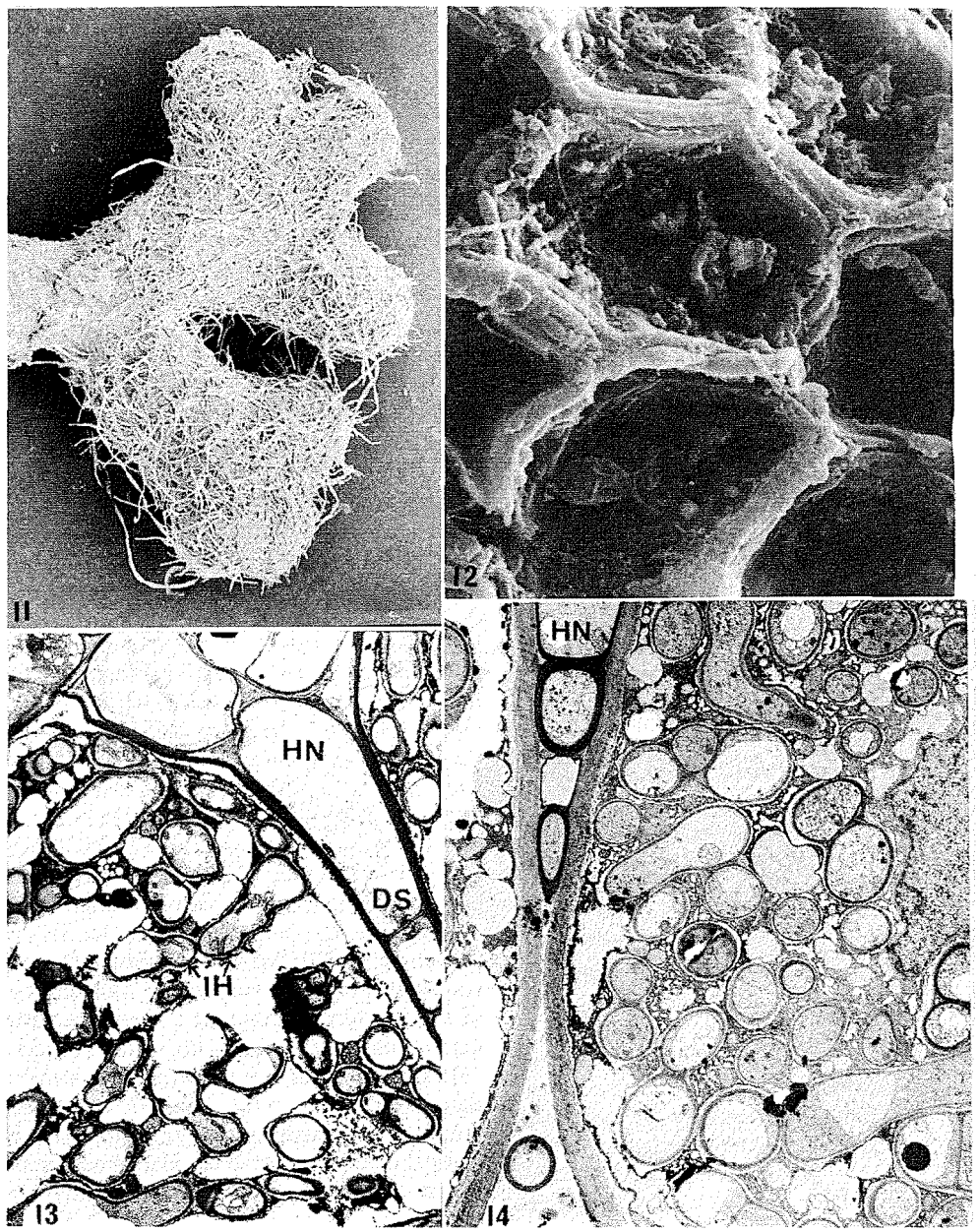


FIG. 11. Scanning electron microscope view of mycorrhizal lateral of *Arctostaphylos uva ursi* showing well-developed sheath. ×100. FIG. 12. Scanning electron microscope view of part of the surface of a mycorrhizal root of *Pyrola rotundifolia* ssp. *maritima* showing absence of sheath but presence of hyphae along the radial walls of the root cortical cells. ×1000. FIG. 13. Transmission electron microscope view of transverse section of *Arctostaphylos* root showing well-developed Hartig net (HN) and intracellular infection (IH) of the cortical cells. A dolipore septum (DS) is seen in one of the Hartig net hyphae. The highly vacuolate nature of both host and endophyte indicates that the infection is past maturity. ×3600. FIG. 14. Transmission electron microscope view of transverse section of *Pyrola* root showing Hartig net (HN) and intense intracellular infection. A dolipore septum is seen in one of the intracellular hyphae. ×4000.

plants of the Monotropaceae have fascinated biologists since the early studies of Unger (1840). The roots of *Monotropa* were first recognized as being truly mycorrhizal by Kamienski (1881, 1882), who described the presence of a sheath and Hartig net comparable with that seen in *Fagus*. MacDougal (1899) observed the presence of a peculiar peg-like structure, which he called a "haustorium" in the outer cortical cells of mycorrhizal roots of *Monotropa* and this structure has since become recognized as the characteristic feature of the *Monotropa* mycorrhiza (Francke 1934). It was considered that the "haustorium" arose as a result of the encapsulation of the invading fungal hypha by a callose-like material Such a process by itself, however, would not be unique, since a similar phenomenon is commonly observed in ericoid infections (Friesleben 1936; Brook 1952; Burgeff 1961).

Ultrastructural analysis has revealed the distinctive nature of the peg in *Monotropa*. Lutz and Sjolund (1973) analysed mature infected cells of *Monotropa* by TEM and were the first to point out that the intrusive element was not a true haustorium because the host cell wall is never actually penetrated. The differentiation of the fungal peg has recently been followed and related to different stages of shoot development by sampling throughout the year (Duddridge and Read 1982*a*). These studies have confirmed that the fungal hyphae do not penetrate beyond the peg during the active life of the association. Rather, the host cell wall around the peg proliferates to form a structure strongly reminiscent of a transfer cell (Pate and Gunning 1972). The absence of true fungal penetration combined with the presence of transfer cell characteristics together justify a differentiation between this type of mycorrhiza, for which the term "monotropoid" is proposed by Duddridge and Read (1982*a*), and the arbutoid type, in which extensive internal proliferation of the fungus occurs.

Effects of ericoid mycorrhizal infection on growth

Several early studies revealed that seedling development was inhibited on peat which had been sterilized by autoclaving. The experiments of Friesleben (1936) led him to the conclusion that the major effect of the mycorrhizal fungus was to detoxify the peat. However, this attribute was not exclusively shown by the mycorrhizal fungus, since a range of saprophytic fungi had the capacity to alleviate the toxicity. Similar results were obtained by Bain (1937) and Burgeff (1961). Thus, until recently, mycorrhizal infection has been considered to be of little significance to the plant except perhaps in the establishment phase. It has been suggested that during the major part of the plant's life the fungus is present as a weakly parasitic associate. However, the relatively massive fungal presence in the ericoid mycorrhizal root must constitute a significant drain on the plant's reserves of carbon and it seems unlikely that the hosts could sustain this drain and maintain their great competitive vigour in the nutrient-stressed heathland habitat if the flow of nutrients was purely unidirectional. Work of Brook (1952) and Morrison (1957) using *Pernettya* provided the first indication that mycorrhizal infection might stimulate yield in ericoid plants, but their results were again confounded to some extent by the use of autoclaved soil and by their failure to obtain pure endophyte inoculum, which in turn led to variable infection levels in mycorrhizal plants.

Since all natural heathland soils contain ericaceous endophytes, some sterilization treatment is required so that control plants can be grown in the nonmycorrhizal condition. In view of their failure to grow normally on autoclaved soil, a superior sterilization treatment has been sought. The most suitable soil sterilization procedure so far found is γ-irradiation (Stribley et al. 1975). Soils sterilized by this method are nontoxic and complete removal of potential endophytes can be obtained with relatively small doses of radiation (0.8 mrads (1 rad = 10 mGy)). The development of large-scale commercial irradiation facilities made possible the systematic analysis of the response of ericaceous plants to inoculation with the mycorrhizal endophytes isolated by Pearson and Read (1973). Early experiments in small volumes of irradiated soil demonstrated that mycorrhizal plants produce greater yields and have significantly higher nitrogen and phosphorus contents than nonmycorrhizal controls (Read and Stribley 1973). There are thus some parallels between the responses of ericaceous plants and those of ectomycorrhizal trees to infection. An important feature of the results obtained was the very marked stimulation of plant nitrogen content in both *Calluna* and *Vaccinium*.

It was of particular interest to learn whether the enhanced nitrogen contents of the mycorrhizal plants arose simply as a result of an improved capacity to capture mineralized nitrogen or whether the fungus could absorb, assimilate, and transfer nitrogen sources which were too complex to be utilized by plant lacking the endophyte. An attempt was made to label the organic constituents of heathland soil by incubation in the presence of added ^{15}N-labelled ammonium sulphate (Stribley and Read 1974). When *Vaccinium* plants were grown on the soil in the mycorrhizal and nonmycorrhizal conditions, the usual stimulation of growth and enhancement of total nitrogen content was found in the mycorrhizal plants, but the amount of labelled nitrogen in these plants was lower than that in the nonmycorrhizal group (Table 2). Analysis of the soil revealed that little of the label had been incorporated into organic material and it was therefore concluded that lower levels of the isotope in mycorrhizal plants were attributable to their having access to the unlabelled organic nitrogen pools. Since

TABLE 2. Nitrogen content and yield and ^{15}N excess of shoots of mycorrhizal (M), nonmycorrhizal (NM), and nonmycorrhizal saprophyte-inoculated (SAP) plants of *Vaccinium macrocarpon* after 6 months growth on ^{15}N-labelled soil (from Stribley and Read 1974)

Growth stage	N content (% oven-dry weight)	Yield (mg oven-dry weight)	Total N (mg/plant)	^{15}N excess (atom %)
Sterile seedlings	0.94	4.23	0.04	0
Plants 6 months after inoculation				
Mycorrhizal (M)	1.20	30.32+	0.36+	15.38+
Nonmycorrhizal (NM)	0.98	20.97+	0.21+	20.03+
Inoculated with:				
Trichoderma sp. } SAP	0.94	18.80	0.18	ND
Aspergillus sp. } SAP	0.82	16.20	0.18	ND

NOTE: Each figure represents a mean of 14 plants, except at stage one, where 30 plants were analysed; +, figures significantly different within the growth at $p < 0.001$; *nd*, not determined.

organically complexed nitrogen sources represent by far the greatest reserve of N in heathland soils, this observation may be of great importance. However, further elucidation of the nature of the nitrogen compounds utilized by mycorrhizal plants grown in peat of mor (humus) is difficult because of the chemical complexity of the medium. For this reason later experiments have examined the growth and nutrition of mycorrhizal and nonmycorrhizal ericaceous plants in sand to which individual organic or mineral constituents have been added.

Experiments in sand

In sand culture containing standard nutrient solutions and nitrogen supplied as ammonium in logarithmically increasing quantities (Stribley and Read 1976), mycorrhizal plants had higher yields and nitrogen contents than the nonmycorrhizal ones at intermediate levels of N supply (Fig. 15). Thus, while no growth stimulus was found in mycorrhizal plants at 1, 20, or 50 mg N/L, significant growth enhancement is found at 2.7 and 7.5 mg/L. The failure to find a growth response at 1 mg/L is interesting. It probably indicates that the benefits derived from infection at such low levels of N do not counterbalance the fungal drain on plant assimilates. At the highest levels of ammonium application the supply of N to the roots of nonmycorrhizal plants was obviously sufficient to sustain optimal growth. However, such luxury levels of N are rarely experienced by plants growing in the field, where levels of free ammonium are more normally in the range in which a mycorrhizal enhancement of growth was observed. Further experiments have compared the capacity of mycorrhizal and nonmycorrhizal plants to utilize NH_4 and a range of amino acids as N sources (Stribley and Read 1980). These were supplied at equivalent concentrations in acid-washed sand, which was maintained in the sterile condition. The results (Table 3) indicate that

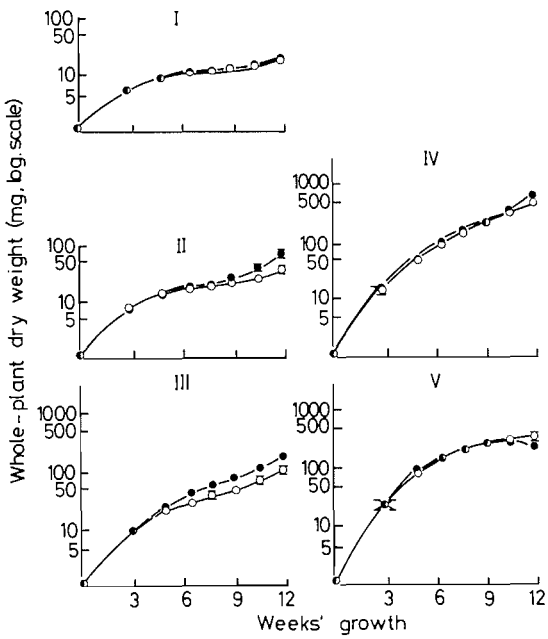


FIG. 15. Yield of M and NM *Vaccinium* plants grown at different levels of ammonium: I, 1 mg/L; II, 2.7 mg/L; III, 7.5 mg/L; IV, 20 mg/L; V, 50 mg/L. ●, M plants; ○, NM plants (from Stribley and Read 1974).

whereas mycorrhizal plants can use most of the organic N sources as readily as the mineral source, the nonmycorrhizal plants have a very limited capacity to use these substances. The capacity to assimilate organic N is specifically a feature of mycorrhizal infection, since plants grown in sand inoculated with some commonly occurring soil saprophytes (SAP), like those in the nonmycorrhizal category, showed no comparable utilization.

These studies have used European plants and soils, but less intensive analyses of African heath species

TABLE 3. The effects of different nitrogen sources on shoot dry weight (milligrams per pot) of *Vaccinium macrocarpon* in mycorrhizal (M), nonmycorrhizal sterile (NM), and nonmycorrhizal nonsterile (SAP) condition

Nitrogen source (20.5 mg/L)	Treatment		
	M	NM	SAP
Ammonium	43.4	41.4	—
Glycine	43.9*	11.6	11.4
Alanine	47.6*	22.5	9.4
Aspartic acid	29.5*	7.0	8.1
Glutamic acid	39.4*	8.2	9.7
Glutamine	44.6*	18.2	23.3
No nitrogen	6.0*	8.3	8.7

NOTE: —, not tested.
*Significant difference in dry weight between M and both other treatments at $p < 0.05$ (Stribley and Read 1980).

suggest that the mycorrhizas are structurally and functionally comparable with those found in Europe, despite the fact that some of the climatic and ecological features are different.

The genus *Erica* reaches its greatest level of species diversity in southern Africa, but the conservatism of form shown by the ericoid root system is retained. Examination of root systems of Cape *Erica* species during the wet winter months reveals that the mycorrhizal associations are structurally identical with those of European representatives of the genus and that the isolated mycorrhizal fungus has similar cultural characteristics. The climate of the Cape region is characterized by a marked seasonality, mild wet winters being followed by hot dry summers. One of the puzzling aspects of the biology of many Cape *Ericas* is that maximum growth, as well as flowering and seed set, coincides with the dry period of the year. Study of their root systems during this period shows that, in contrast with the winter conditions, they have a moribund appearance, with collapsed cortical cells. As part of an experimental analysis of this situation (Read 1978), plants of the Cape heath species *Erica bauera* were grown from seed in the mycorrhizal and nonmycorrhizal condition in a soil with supraoptimal nitrogen concentrations. They were then transferred to sand, in which they were grown for a further 4 weeks and supplied with a mineral nutrient solution lacking nitrogen. Shoots of both mycorrhizal and nonmycorrhizal plants were harvested at weekly intervals through the 4 weeks and their N contents were determined. During this period the nitrogen contents of the nonmycorrhizal plants declined progressively, while those of the mycorrhizal plants was sustained (Fig. 16). Microscopic analysis of the root systems of harvested mycorrhizal plants revealed that during the 4 weeks of growth in the absence of nitrogen the level of infection decreased markedly. It was therefore concluded that nitrogen contents of the shoots of mycorrhizal plants were sustained by transfer of nitrogen stored in the hyphal complexes of the root cortical cells. These results indicate that in addition to provision of enhanced uptake and increased access to recalcitrant forms of N, the mycorrhizal fungus may act as a store of seasonally released nutrients, which can later be used to sustain growth during unfavourable climatic conditions.

Ericoid mycorrhizas and heavy metal resistance

While it is now well established that mycorrhizal infection can lead to increased efficiency of nutrient capture in nutrient poor environments, relatively little attention has been given to the role of mycorrhizas in soils containing elevated and potentially toxic levels of mineral elements. It is clear that if mycorrhizal infection leads to enhancement of uptake in these circumstances, the results would be physiologically damaging rather than beneficial to the host. Ericaceous plants are particularly successful colonists of habitats both natural and manmade which have elevated levels of metallic elements. Natural heathland soils are characterized by their low pH and associated with this acidity is an increase in the availability of metals like aluminium and copper to levels which become toxic to many nonericaceous species. On the most acid of these soils ericaceous plants are often the sole dominants. In addition to their success in these natural circumstances, plants like *Calluna* are sometimes the only colonists of acid spoils produced by copper- and zinc-mining activities in Europe (Marrs and Bannister 1978; Oxbrow and Moffatt 1979), while *Vaccinium* and *Gaultheria* are prominent on soils contaminated by smelting in Canada (Freedman and Hutchinson 1980). Recent studies (Bradley et al. 1981, 1982) suggest that mycorrhizal infection may play a key role in providing resistance to heavy metals in *Calluna*, *Vaccinium*, and *Rhododendron*. Plants of each species were grown in the mycorrhizal and nonmycorrhizal condition in sand cultures with a dilute nutrient solution which was supplemented with either copper as copper sulphate at 0, 10, 15, 50, and 75 mg/L or zinc as zinc sulphate at 0, 25, 50, 100, and 150 mg/L. These are the most common metalliferous contaminants of mine spoils and in each case the concentrations selected range from low to extremely high levels of the available mineral element. Little or no growth occurred in the nonmycorrhizal plants of any species at any treatment level and in some of the higher metal levels mortality was considerable. Some growth reduction also occurred in mycorrhizal plants at all metal levels, but only at the highest metal concentrations was a major growth reduction seen (Figs. 17–22). The concentrations of the test metals in the shoots were determined and polynomial regression analysis of the data revealed that in all but one case levels of metal accumulation were significantly

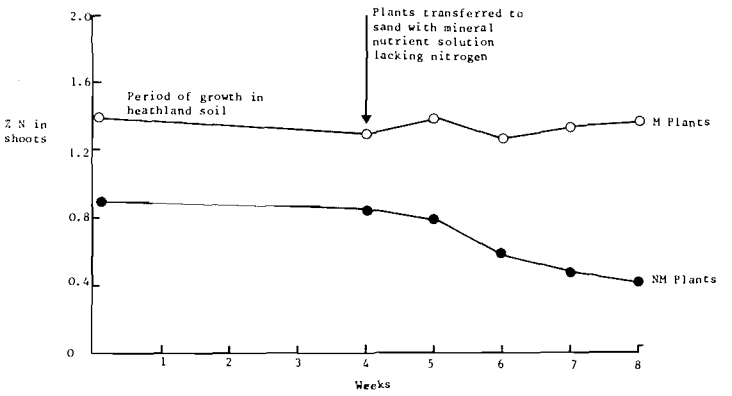


FIG. 16. The effect of nitrogen starvation on shoot nitrogen content in M and NM plants of *Erica bauera* (from Read 1978).

lower in the shoots of mycorrhizal plants. It seems therefore that whereas in the absence of the mycorrhizal fungus the plant is unable to exclude the metal which accumulates in the shoots to toxic levels, mycorrhizal infection provides the capacity for exclusion of metals from shoots and thus for avoidance, sensu Levitt (1980), of metal toxicity. When pure cultures of the individual mycorrhizal endophytes were grown in liquid cultures containing the metals, none showed inhibition of growth over the range used in the sand culture experiments. It was concluded that exclusion of metals in mycorrhizal plants was attributable to adsorption of metallic ions by the actively growing fungi in the host cortical cells. Evidence for such a conclusion was obtained in the form of elevated metal levels in the roots of the mycorrhizal plants. The possible nature of the adsorptive mechanism and ecological significance of these observations are discussed later.

Observations on the availability of N and P sources to the ericoid endophyte in pure culture

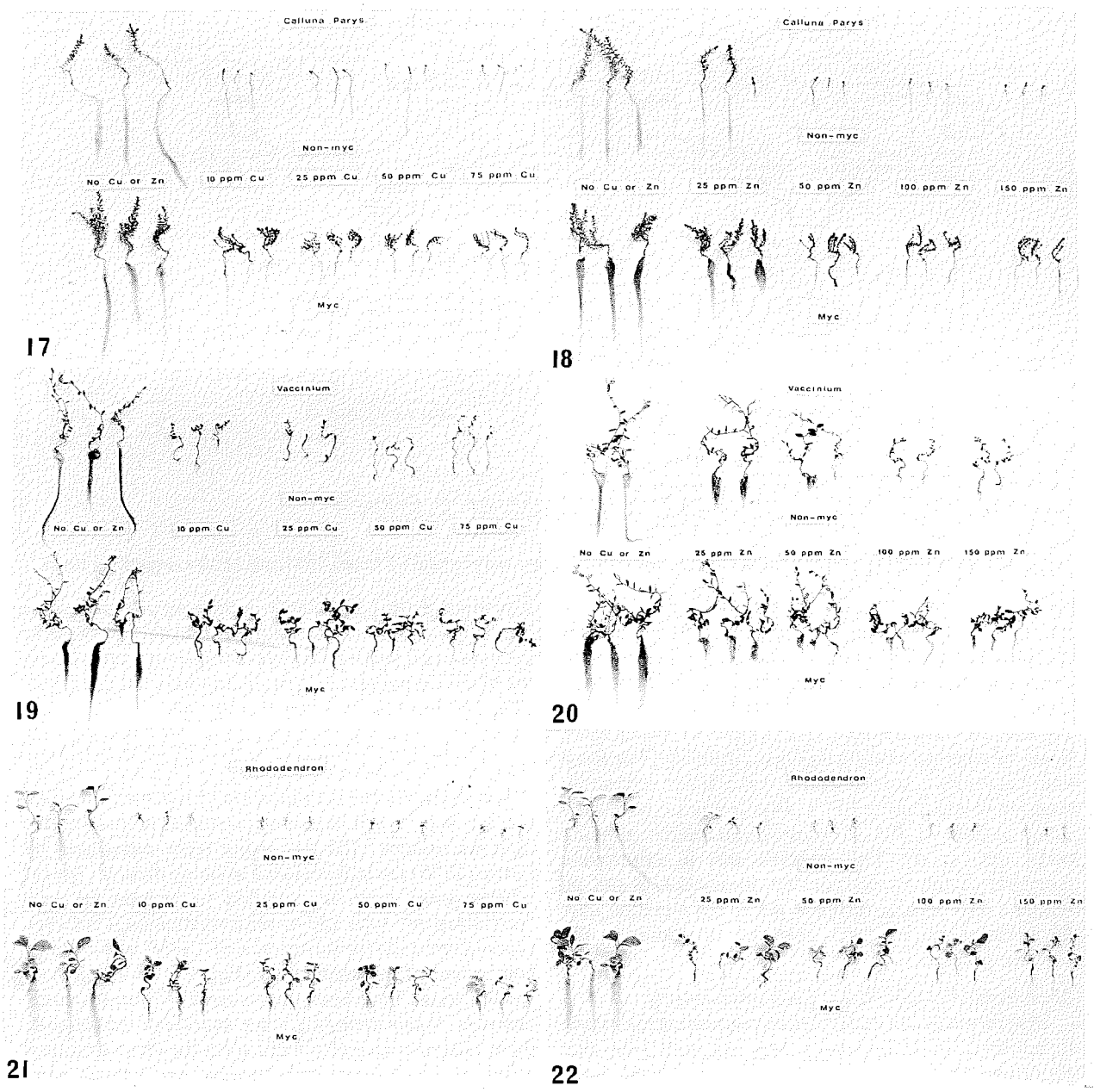
Liquid culture experiments have confirmed that ericoid mycorrhizal endophytes from a range of host species will utilize simple organic nitrogen sources (Pearson and Read 1975). Under these circumstances, however, the fungus showed no capacity to use either humic or fulvic acids as sources of nitrogen or carbon (Stribley and Read 1980). This does not rule out the possibility that when in combination with the host plant the availability of carbon as a substrate for enzyme production may facilitate some degradation of these more complex sources. This matter is at present under experimental observation.

Relatively little attention has been paid to the possible role of mycorrhizal infection in the phosphate nutrition of ericoid mycorrhizas. It has been observed, however, that P as well as N levels are enhanced in mycorrhizal plants (Read and Stribley 1973) and since mor soils have large reserves of organic P as well as of N, mycorrhizal infection could be of importance if it provides access to these reserves. The ratio of organic to total P in such soils varies (Cosgrove 1967) but is usually high. A major proportion of this organic P is in the form of inositol hexaphosphate, which is present largely as insoluble phytate salts (Martin and Cartwright 1971; Anderson et al. 1974; Cheshire and Anderson 1975; Cosgrove 1980). It is likely that in acidic heathland soils aluminium and ferric phytate salts will predominate. These salts have been synthesized by Mitchell and Read (1981) and used as sole phosphate sources in studies of the utilization of organic and inorganic P by ericoid endophytes from different host species. At a concentration of 100 mg P / L, yields of each endophyte were comparable with those obtained on inorganic P at the same concentration. Mycorrhizal seedlings of *V. macrocarpon* were also shown to grow better than nonmycorrhizal at 1 mg/L of orthophosphate. In nature therefore infected plants should be able to benefit both in terms of enhanced uptake of mineral P and of organic P. Quantification of these benefits will be a fruitful area for future research and it is important in this connection to be aware that some organic P sources may be available to uninfected higher plants (Wild and Oke 1966).

Transmission electron microscopy studies reveal that absorbed phosphate can be stored and presumably transported as polyphosphate granules in hyphal vacuoles. This suggests that the mechanisms of phosphate storage and mobilization may be comparable with those seen in vesicular–arbuscular (VA) (Cox *et al.* 1975) and ectomycorrhizas (Ling Lee *et al.* 1975).

Arbutoid mycorrhizas, functional aspects

While direct experimental information on the role of arbutoid mycorrhizas is lacking, the similarities of structure and the close taxonomic relationships between causal fungi both suggest that they will be functionally comparable with ectomycorrhizas. The fungal sheath, when present, will supply the storage function observed by Harley (1969) and the associated



FIGS. 17–22. Representative plants of the three test species *Calluna vulgaris*, *Vaccinium macrocarpon*, and *Rhododendron ponticum* after growth in the mycorrhizal (MYC) or nonmycorrhizal (NON-MYC) condition for 12 weeks at different levels of copper or zinc.

basidiomycete hyphae will provide a more extensive exploitation of the upper soil horizons than that seen in ericoid infections. As in the case of ectomycorrhizas, elaborate mycelial systems with fans and rhizomorphs have been observed in association with arbutoid roots (Luck 1940; Lihnell 1942; D. J. Read, unpublished data). It is known that such systems will absorb both organic (Melin and Nilsson 1953) and inorganic (Melin and Nilsson 1952) nitrogen sources, phosphate ions (Bowen 1973), and water (Duddridge *et al.* 1981) and that they facilitate their transfer to the ectomycorrhizal root. A similar role would be expected in arbutoid mycorrhizas.

The question of the role of arbutoid mycorrhizas in carbon transport becomes of great interest in those members of the *Pyrolaceae* which are achlorophyllous.

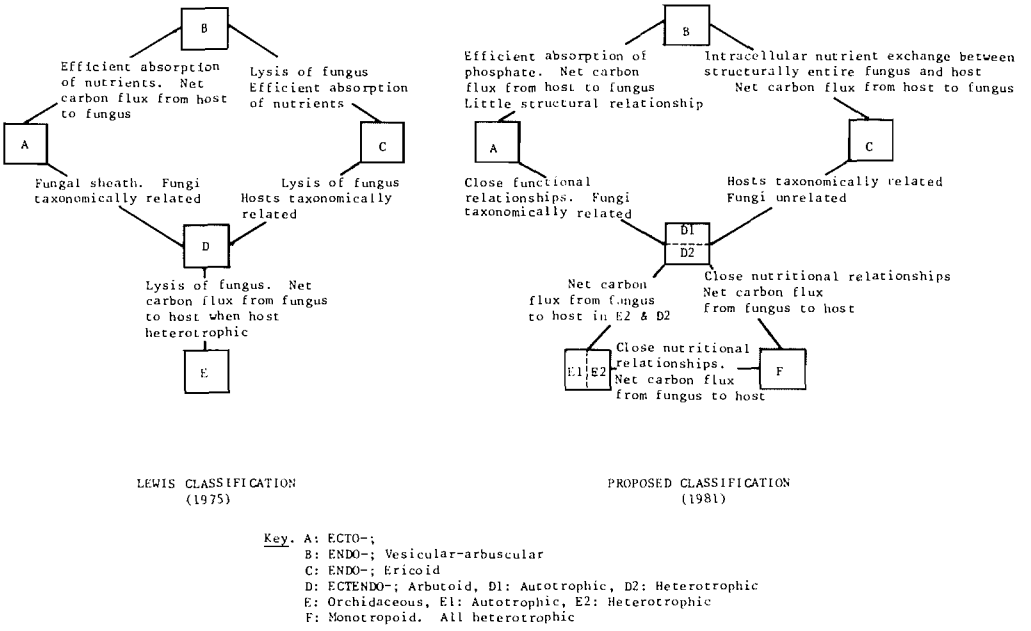

B
Efficient absorption of nutrients. Net carbon flux from host to fungus
Lysis of fungus Efficient absorption of nutrients
A
C
Fungal sheath. Fungi taxonomically related
Lysis of fungus Hosts taxonomically related
D
Lysis of fungus. Net carbon flux from fungus to host when host heterotrophic
E
LEWIS CLASSIFICATION (1975)
B
Efficient absorption of phosphate. Net carbon flux from host to fungus Little structural relationship
Intracellular nutrient exchange between structurally entire fungus and host Net carbon flux from host to fungus
A
C
Close functional relationships. Fungi taxonomically related
Hosts taxonomically related Fungi unrelated
D1
D2
Net carbon flux from fungus to host in E2 & D2
Close nutritional relationships Net carbon flux from fungus to host
E1
E2
Close nutritional relationships. Net carbon flux from fungus to host
F
PROPOSED CLASSIFICATION (1981)
Key. A: ECTO-;
B: ENDO-; Vesicular-arbuscular
C: ENDO-; Ericoid
D: ECTENDO-; Arbutoid, D1: Autotrophic, D2: Heterotrophic
E: Orchidaceous, E1: Autotrophic, E2: Heterotrophic
F: Monotropoid. All heterotrophic

FIG. 23. Interrelationships between the major mycorrhizal types as proposed by Lewis 1975 and as now revised by Read.

All members of this family appear to be largely though not exclusively associated with ectomycorrhizal trees or shrubs in nature. The functional basis of this association is not understood, but it is true that in such ecosystems the tree roots may be the only source of inoculum for mycorrhiza development. The extent of dependence upon the tree has been the subject of debate, but Read and co-workers (unpublished data) have repeatedly failed to detect transfer of ^{14}C-labelled assimilates from *Salix* bushes to *Pyrola rotundifolia* plants growing under the canopy. This suggests that in autotrophic members of the Pyrolaceae the association is not an obligate one. In heterotrophic plants the situation may be different, as has been revealed in studies in the Monotropaceae.

Monotropoid mycorrhizas, functional aspects

Despite much early speculation concerning the role of mycorrhizas in *Monotropa* it was not until 1960 that Björkman first demonstrated that mycorrhizal fungi provided direct functional connections between the tree roots and those of *Monotropa* (Björkman 1960). Movement of phosphate as ^{32}P and of carbon as ^{14}C was demonstrated from autotroph to heterotroph. Björkman made the important observation that older plants took up less ^{14}C than those in which the flowering spike was still developing. This is consistent with the pattern of development of transfer cells in young plants (Duddridge and Read 1982*a*). Furman (1966) and Duddridge (1980) have since confirmed the movement of these isotopes between the two plant partners. A number of interesting features of the association remain to be investigated. In particular it is necessary to determine the factors which initiate nutrient transfer, to examine the nature and major pathways of transport, and to assess the relative amounts of nutritional support obtained from litter and from the associated autotroph.

Discussion

Until recently the classification of mycorrhizal structure has been based largely upon studies employing the light microscope. The five major types recognized by Lewis (1975) are still accepted as being distinct, but his scheme must now be modified to include the new "monotropoid" type and to omit relationships between types based upon the occurrence of "lysis" of the fungal component of the association (Fig. 23). Both of these modifications have been necessitated by ultrastructural analyses. While changing some aspects of the scheme, these analyses have also made clear the close structural affinities which occur both between mycorrhizal types and at a wider level between mutualistic and biotrophic associations. These affinities are most clearly seen at the host–fungus interface. This zone, with its interfacial matrix, is comparable in structure in ericoid and arbutoid infections, in mycorrhizas of the Orchidaceae (Dorr and Kollman 1969; Hadley *et al.* 1971; Nieuwdorp 1972; Strullu and Gourret 1974), and in the arbuscule of VA mycorrhizas (Scannerini and Bellando 1968; Kaspari 1975; Cox and Sanders 1974; Kinden and Brown 1975*b*, 1976). Most workers now agree that the matrix material in these associations is of host origin and positive staining using Thiery's (1967) method has

confirmed the polysaccharide nature of the matrix in ericoid (Duddridge 1980), VA (Dexheimer et al. 1979; Scannerini and Bonfante-Fasola 1979), and orchidaceous (Strullu and Gourret 1974) mycorrhizas. Though no intracellular fungal penetration normally occurs in ectomycorrhizas, a zone which has similar properties is found between the host cell wall and the fungal hyphae of the Hartig net. This area, which has been called the "involving layer" (Scannerini 1968), may arise from depolymerisation of host cell wall material and again it appears to have a high pectin content. Both interfacial matrix and involving layer are seen in arbutoid mycorrhizas.

It is now believed that lysis of the intracellular endophyte is not the basis of the nutrient transfer process in ericoid mycorrhizas and a similar view has been reached from ultrastructural studies of VA mycorrhizas (Cox et al. 1975; Cox and Tinker 1976). Since large-scale digestion of the fungus does not occur in these associations, nutrient exchange between fungus and host must take place during the period when the two partners have structural integrity, and the interfacial matrix must be the zone across which the major transfer processes occur. The process of transfer is not yet understood and the fact that in most mutualistic associations a bidirectional flow must occur indicates that the mechanism may be complex. Recent studies of the membranes surrounding the haustoria of a biotrophic parasite (Spencer-Phillips and Gay 1981) have shown that they have distinctive enzyme characteristics which may provide for increased permeability. This feature together with the presence of pectic materials in the interfacial matrix may help to provide conditions conducive to the maintenance of efficient nutrient flux between host and fungus. At the ultrastructural level there are other similarities between the arbuscule of VA mycorrhizas and the hyphal complexes forming the infection unit within the ericoid cortical cell. The formation of both structures is associated with increased quantities of host cytoplasm (Kaspari 1975; Cox and Tinker 1976; Duddridge and Read 1982*b*). Numbers of cell organelles including mitochondria, ribosomes, and rough endoplasmic reticula proliferate extensively in arbuscule-containing cells and in ericoid infection units (Cox and Sanders 1974; Kinden and Brown 1975*a*, 1975*b*; Duddridge and Read 1982*b*). All these features suggest intensive physiological activity and lend support to the view that the major functional phase of the association in both cases lasts for the short period after infection during which fungus and host maintain structural integrity. The requirement in these, as in the other cases examined, for efficient transfer between partners over a limited time span has apparently led to the selection of similar structural features in a wide range of host–fungus associations.

While these structural similarities may provide increased efficiency of nutrient transfer, analysis of the literature suggests that there are some distinct qualitative differences in the nature of the substances moved in the different types of mycorrhizal association. Whereas VA infection primarily enhances the flux of P into the host plant (Tinker 1975), the arbuscule being the site of transfer of inorganic P to the host cell (Shoknecht and Hattingh 1976), the major effect of ericoid infection is enhancement of host nitrogen content (Read and Stribley 1973). Ectomycorrhizas and probably also arbutoid mycorrhizas appear to occupy an intermediate position, in that while their primary role is concerned with increased uptake and storage of phosphate (Harley 1969), it is known that they also absorb and transport both ammonium (Melin and Nilsson 1952) and amino (Melin and Nilsson 1953) nitrogen sources, though they use nitrate less readily (Carrodus 1967). Some of these differences, particularly, for example, the predominant role of VA infection in P absorption may reflect the emphasis of research activities rather than the field situation, but nonetheless they can provide a working basis for some assessment of the ecological role of the distinct mycorrhizal types.

It is now becoming clear that each type of mycorrhiza is characteristically associated with a specific set of soil circumstances and it is therefore likely that the functional differences between them have been selected in response to the particular nutrient stresses of the habitat. This suggests that the infection plays a vital role in the ecosystem. Three more or less distinct types of ecosystem can be recognized each with its own soil–mycorrhizal characteristics but with transitions occurring between the types (cycles A, B, C, Fig. 24).

Ericoid mycorrhizas (cycle A) are almost exclusively restricted to soil in which the bulk of the nutrient fund is contained in recalcitrant organic form and only a small fraction is in the vegetation (Robertson and Davies 1965). The soil type is a product of a cyclical sequence of events which maintain its characteristic features and produce a stable "climax" vegetation. In the case of heathland soils low nutrient availability leads to the production of tissues with low N and P levels and hence low protein contents. In these circumstances carbon is assimilated into a range of secondary metabolites, prominent among which are aliphatic and polyphenolic acids and lignins. Such substances accumulate in leaves which are often small or needlelike and have a sclerophyllous habit (Loveless 1962). Structures of this kind are so typical of the Ericaceae that they have been called "ericoid" leaves (Specht 1979). The litter produced by these leaves contains few readily soluble organic or inorganic nutrients because N is precipitated in stable polyphenol–protein complexes, has a high C:N ratio, and low pH. It thus maintains or even accentuates mor

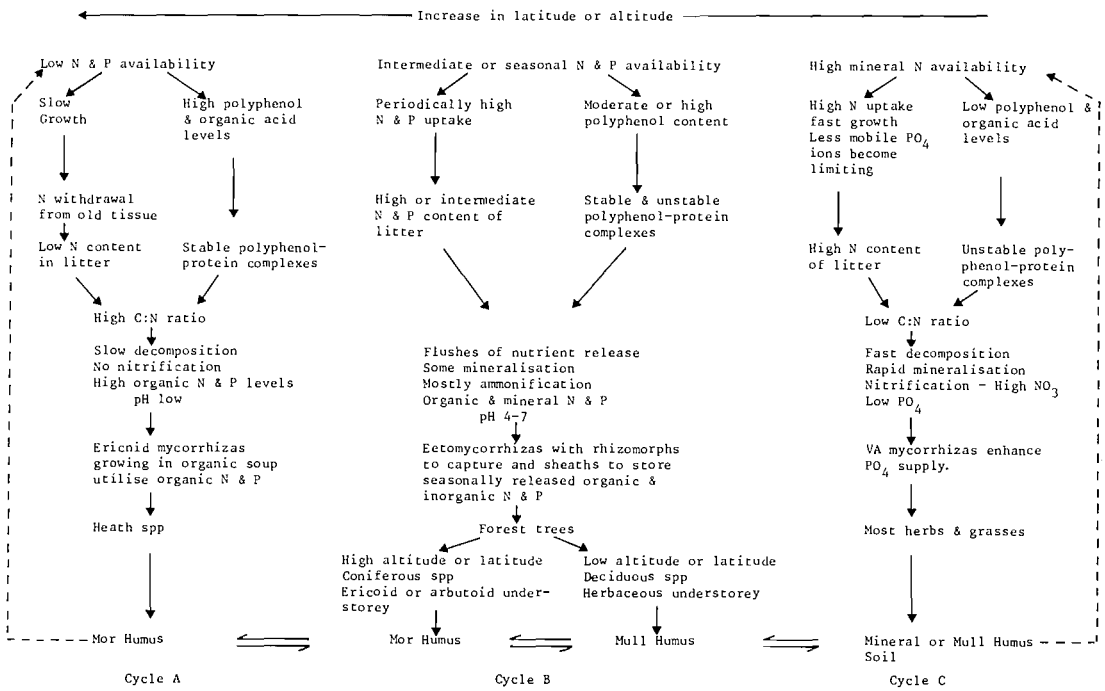

Increase in latitude or altitude
Low N & P availability
Slow Growth
High polyphenol & organic acid levels
N withdrawal from old tissue
Low N content in litter
Stable polyphenol-protein complexes
High C:N ratio
Slow decomposition
No nitrification
High organic N & P levels
pH low
Ericoid mycorrhizas growing in organic soup utilise organic N & P
Heath spp
Mor Humus
Cycle A
Intermediate or seasonal N & P availability
Periodically high N & P uptake
Moderate or high polyphenol content
High or intermediate N & P content of litter
Stable & unstable polyphenol-protein complexes
Flushes of nutrient release
Some mineralisation
Mostly ammonification
Organic & mineral N & P
pH 4-7
Eetomycorrhizas with rhizomorphs to capture and sheaths to store seasonally released organic & inorganic N & P
Forest trees
High altitude or latitude
Coniferous spp
Ericoid or arbutoid under-storey
Low altitude or latitude
Deciduous spp
Herbaceous understorey
Mor Humus
Mull Humus
Cycle B
High mineral N availability
High N uptake fast growth
Less mobile PO4 ions become limiting
Low polyphenol & organic acid levels
High N content of litter
Unstable poly-phenol-protein complexes
Low C:N ratio
Fast decomposition
Rapid mineralisation
Nitrification - High NO3
Low PO4
VA mycorrhizas enhance PO4 supply.
Most herbs & grasses
Mineral or Mull Humus Soil
Cycle C

FIG. 24. Ecosystem interactions leading to the prevalence of destinctive vegetational mycorrhizal and soil characteristics of three types.

conditions. Plants with the capacity to obtain access to slowly released organic N and P compounds are likely to be most successful under these circumstances. It is known that free amino acids occur in soils of this type (Dadd *et al.* 1953; Sowden and Ivarson 1966) and that, in cold areas where ammonification is inhibited, they can even accumulate (Labroue and Carles 1977). Studies of Persson (1978) have confirmed that most of the fine ericoid roots in morhumus soil are concentrated in the humic surface horizons. Here they are bathed in a colloidal medium containing carboxylic acids and a range of complex and simple organic N and P molecules. Further information on the nature of these organic moieties and on the extent of their availability to the mycorrhizal plants is now being sought, but evidence obtained so far confirms that the simplest of the organic N and P sources can be used by the ericaceous plants in the mycorrhizal condition (Stribley and Read 1980; Mitchell and Read 1981).

Where environmental circumstances are less severe, for example, with decreasing altitude or latitude, mineralization processes become more rapid (cycle B, Fig. 24). In the early part of the transition from cycle A to B the dominant plants, usually coniferous species, are still sclerophyllous, and on the mor soils underneath their canopies plants with ericoid mycorrhizas, in particular *Vaccinium* species, are often an important component of the vegetation. These may here be mixed with plants like *Pyrola* and *Arctostaphylos* having arbutoid mycorrhizas. With further environmental amelioration deciduous trees become prominent. In general these produce litter with a higher total N and P content and with a greater quantity of readily soluble organic constituents (Nykvist 1963). Decomposition and nutrient turnover are therefore more rapid and a trend towards mull (humus) formation is found. In soils with mull rather than mor-humus, plants with VA mycorrhizas replace those with the ericoid type in the ground-layer community.

Most of the dominant plants in boreal coniferous and temperate deciduous forest ecosystems have ectomycorrhizas with fungal associates, often basidiomycetes, forming extensive mycelial systems exploiting the litter and other well-aerated zones of the soil throughout the growing season (Bowen 1973; Duddridge *et al.* 1981). Here the fungi are also in a position to absorb the ammonium and simple organic nutrients released from the litter by seasonal flushes of microbial activity (Harley 1978). Nutrients thus collected can be stored in the sheath and released slowly for subsequent utilisation by the host plant.

Vesicular–arbuscular mycorrhizas become dominant in soils in which active mineralization processes are taking place (cycle C, Fig. 24). These processes yield sufficient ammonium or nitrate to permit rapid growth, but because of the relative immobility of the phosphate

ion, the rhizosphere region can become depleted of P (Lewis and Quirk 1967; Bhat and Nye 1974). Hyphae of VA mycorrhizas grow beyond these depletion zones and capture phosphate ions, which are then translocated to the plant probably as polyphosphate granules (Cox *et al.* 1975; Tinker 1975). This type of mycorrhiza becomes particularly prominent in phosphate-deficient grassland communities (Read et al. 1976). While each type of cycle has distinct qualities, there are, of course, zones of transition between them in which all mycorrhizal types may occur together. Such circumstances may indicate instability in the ecosystem with changes occurring in the direction of mull or mor formation.

An important characteristic of mor-humus soils is the increased availability of metallic cations like aluminium, copper, and zinc caused by low pH. This increase is sufficient to render the soils toxic to many plants (Rorison 1973). The resistance to these metals provided by ericoid mycorrhizal infection (Bradley *et al.* 1981, 1982) is likely to be of great ecological importance and it is necessary to consider the possible mechanism of exclusion of such metallic elements from the plant. Studies on metal binding in another mutualistic association provide some indication of the possible adsorption mechanism. In lichens, metal ions taken up from solution are bound reversibly through an ion-exchange process (Nieboer *et al.* 1976). The occurrence of functional groups suitable for metal binding and having a pK_a between 2 and 7 has been demonstrated by these workers. Tuominen (1967) indicated that these functional groups were carboxylic acid moieties of pectinlike substances. While the exact location of these binding sites remains to be detected in lichens, results of histochemical and ultrastructural analysis of ericoid mycorrhizas (Duddridge 1980) suggest that such binding sites are likely to be abundant in the interfacial matrix. Thus while providing improved permeability for some ions, divalent and trivalent cations may be effectively bound by the carboxylic acids of the matrix at a critical position in the host–fungus interface. Electron probe and microautoradiographic analyses will be required to determine the precise pattern of localization of metals.

This work makes it clear that interpretation of mycorrhizal benefits in terms of enhancement of uptake of one or two nutrients may greatly oversimplify the situation. There may be a wide range of advantages to the host plant, some of them positive, for example increased nutrient absorption, some negative, as in the case of exclusion of undesirable elements, and there may be other roles which we have not yet detected. Interpretation of the capacity of mycorrhizas to provide successful exploitation of complex environments requires a full understanding of all the possible interactions between host, fungus, and habitat. Our understanding of these interactions in ericoid mycorrhizas is increasing, but experimental analysis of related arbutoid systems has not even begun. The scope for future research is large indeed.

Acknowledgments

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